GENETIC STUDIES ON SOYBEANS

BY

HOU-LEE LIU

B.S., National Central University, China, 1939
M.S., University of Illinois, 1946

AN ABSTRACT OF A THESIS

SUBMITTED IN PARTIAL FULFILLMENT OF THE REQUIREMENTS
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GENETIC STUDIES ON SOYBEANS

The present study was carried on for a period of three years, from February, 1945, to February, 1948. The writer came from China to do research work at the University of Illinois under the kind direction of Professor C. M. Woodworth, who is a world famed soybean geneticist. Under his guidance, hand pollination and various analytic methods for different phases of soybean genetics have been studied by the writer.

The purpose of the present study is to make a general survey on the inheritance of principal characters in soybeans, from which much more information could be gathered and further studies could be easily conducted. This paper is also considered as a detailed presentation and interpretation of genic relationships of soybeans. A large number of crosses were made both in the greenhouse and in the field from 1945 to 1947. F_1, F_2, F_3 were grown for genetic analysis. The X^2 test for goodness of fit was used in such analyses. For facilitating the interpretation of results obtained, the assumptions on the basis of genic relationships were also made, accompanied by complete description of all characters involved.

The characters considered are classed in two groups; namely, plant characters and seed characters. They are all considered to be qualitative inheritance.

A. Inheritance of Plant Characters

This phase of soybean genetics includes a study of morphological structures, as leaf, flower, hair, stem, pod, and also includes a study of the physiological or physio-genetical development, such as growth habit, dwarfness, fasciation, and erectness.

1. *Leaf Characters.*—Three kinds of leaves were classified on their morphological differences and on their inheritance behavior. The na gene is responsible for narrow leaf, while the o gene is responsible for oval leaf. When both of them are present, the na gene is considered to be epistatic to the o gene. However, various degrees of variation from narrow to oval were found in several crosses and these are supposed to be due to the interaction of na with Oo in heterozygous condition, and the same for o gene with Nana in heterozygous condition.

Yellow types and variegation were studied intensively with respect to their behavior in inheritance. The interaction between several genes v_1 (for variegation, as T144), y_8 (for one type of chlorophyll deficiency, as T138 and T144), and y_{10} (for another type of chlorophyll deficiency, as T135), was studied. Gene v_1 causes uneven distribution of chlorophyll in leaf cells from the third compound leaf up, and its effects persist up

to the mature crop. There is no difference between effects of y_8 and y_{10} genes in seedling stage. All yellow seedlings look alike with respect to the degree of yellowing. However, just before the flowering stage, there are important changes in the yellow plants. Certain yellow plants bearing y_{10} retain the same appearance up to maturity, while leaves on the lower portion of the plant of other types change to nearly normal green, only leaving goldenish yellow-green leaves on the top, and these are considered to be the result of the y_8 gene. Plants combining genes for variegation and yellow have been found in F_3. Reduction of plant vigor and plant height was observed.

Wavy leaf type is one of the new characters studied. It is believed that wavy leaf is produced by the combination of two recessive genes (wv_1 and wv_2) for wavy margin on the leaf blade along with the absence of an inhibiting gene, I^{wv}; that is i^{wv}. Or, triplicate genes, wv_1, wv_2, and wv_3 are responsible for the appearance of wavy leaf type. All F_3 results prove this assumption. One cross made with a pure recessive type and a normal parental plant showed a 3:1 ratio, only a single gene difference between the two parents involved.

2. *Hair Characters.*—As to the inheritance of glabrousness, the writer agreed with the results obtained by several workers. But a new system of using symbols for the inhibiting gene was presented in order to avoid confusion. As ordinarily used P_1 stands for inhibiting pubescence, and P_2 for pubescence. Referring to the dominance of pubescence, P is still used for pubescence. But, I^p is suggested as an inhibiting gene to prevent the appearance of hairs on the soybean plant. This system can be adapted to all cases involving inhibiting genes. It consists in putting a small letter of the main gene, as "p," as a superscript to the right and a little above the ordinary symbol "I" for the inhibiting gene.

Hair color is of two kinds, tawny and gray. Tawny (T) is a simple dominant to gray (t), a 3:1 ratio in F_2 being obtained from a number of crosses. However, one cross showed F_1 gray and 3 gray to 1 tawny in F_2. This appeared to be a case of reversal of dominance. Only a few progeny segregated in F_2 into 13 gray to 3 tawny. No F_2 progeny with gray hair segregated into 3 gray to 1 tawny; however, some of F_2 progeny with tawny hair segregated into 3T to 1t. A large number of progeny bred true for t. This fact is probably due to difficulties in the classification of hair color. A fourth class was studied in great detail and involved complementary genes for hair color. Several crosses made between types with t hair, gave tawny in F_1 and 9 tawny to 7 gray in F_2. By X^2 test on F_3 data, the data were a good fit for the assumption. Therefore, both T_1 and T_2 genes are suggested as responsible for the presence of tawny hair. But, by partial dominant action of

either T_1 or T_2 in different phases of plant development, difficulties may be encountered in classification of hair color in F_2 and F_3. Such mixed types have been described by the writer.

Twisted hair is a character which has been observed in a preliminary way. Since the twisting of young hairs occurs at very early stages, they will drop off in late stage of maturity, and the writer considers this may be due to genic control. Its behavior in inheritance was not studied.

3. *Flower Characters.*—As far as flower color is concerned, all results obtained from crosses between the plants with purple flower and the plants with white flower gave a good fit for the general conclusion, that purple (W) was dominant to white (w). However, a particular result was found involving a cross between two whites. F_1 was a purplish flower and produced a 9 purple to 7 white ratio in F_2. By using hypocotyl color as a criterion for judging the flower color, the seedlings were studied in a sandbench in the greenhouse. The result was a good fit for the expected ratio in F_3. However, some deviation in F_3 plants in the field was obtained. Test crosses should be made to determine whether this assumption is true.

Long flower cluster is a characteristic of certain types. A preliminary study was made on its behavior in F_2 and F_3. This character is supposed to be determined by either one or two recessive genes, as fc_1 and fc_2. A very good fit to a ratio of 9 normal to 7 long flower cluster was obtained in F_2.

4. *Growth Habit.*—Growth habit is also referred to as flower-cluster-forming or pod-forming habit. Generally, the plants are indeterminate in growth habit as they make continuous growth as long as conditions are favorable; for plants determinate in growth, the main axis is terminated by the flower cluster. Various characters concerning these two extreme types can be used to distinguish them, such as the period of flowering, the formation of the flower cluster at the tip of the plant, the height of the plant, the maturity, the forms of terminal buds, the standing ability, and the ability for setting on the pods at the tip of the plant.

As to their behavior in inheritance, the indeterminate (Dt) type is generally considered as a simple dominant to the determinate (dt) type. This has been confirmed from F_1 and F_2 plants. However, two groups of results showed reversal of dominance in F_1, one segregating into 3:1 ratio in F_2, while another group segregated into 13:3 ratio in F_2. Gene I^{dt} has been suggested for preventing the plant from making continuous growth, resulting in the determinate habit. Another case involved one cross made between two determinate types. It gave dt in F_1, and 15:1 ratio in F_2, and the indeterminate plants bred true in F_3 generation.

Consequently, one more gene T_f for forming terminal flower cluster has been suggested as a duplicate gene with I^{dt}, and also T_f gene is supposed to be epistatic to the dominant Dt gene. Various possible combinations of these three groups of genes and their behavior in inheritance have been presented in table form.

5. *Dwarfness.*—Dwarfness is a common character for those types bearing the dt gene. By combining several determinate types with ordinary indeterminate types, there were usually found dwarf plants in F_2 and F_3 in very small numbers. These dwarfs are not more than 10 inches in height, bearing 3-4 short branches and a small number of pods. As to their behavior in inheritance, six crosses showed that there are two recessive genes involved for dwarfness. Another group showed three recessive genes concerned. Genic constitutions of various types have been suggested. The most important thing pointed out was their order of flowering in relation to the dt gene or genes. The first flower always blooms on the tip of the plant, being 10-14 days earlier than the normal plant in the same progeny. That is a typical cyme from the taxomonic point of view rather than an ordinary determinate plant. Furthermore, all dwarf plants are determinate in growth, this being considered as either dt gene or genes affecting the growth habit of dwarf plants or genes that are completely linked with the dwarf gene. It may have some importance in the evolution of soybean plants, from the wild indeterminate condition to the determinate cultivated form and finally to dwarfness.

6. *Fasciation.*—Fasciation is a characteristic of some types from Japan. It is a simple mutation from normal (F *vs.* f). All results entirely coincided with Nagai's. A particularly small plant was found with the combination of all recessive genes, f, dt, and df, which might be used for test crosses.

7. *Erectness.*—All cultivated soybeans are erect, short, and branching with a well-developed main stem. But all wild types are non-erect, bearing long stem with distinct twining habit both in the main stem and in the branches. As to behavior in inheritance, non-erectness is dominant to the erectness of cultivated types in F_1 and F_2. All plants in F_2 are quite small; most are non-erect, but several plants tend to be erect, or their main stems become almost erect. Simple dominance of non-erectness has been proposed for this condition. However, one intermediate type, namely Gracilis, showed a reversal of dominance, semi-erectness being recessive to the erectness of cultivated types. Gracilis is considered to be a transitional form which was probably produced from the original wild type.

8. *Pod Characters.*—Classification of pod color types is based upon the coloration of pods at maturity. Three classes of pod color have been made for the study of their behavior in inheritance, namely dark, medium and light. A number of crosses were made between different classes: dark × medium, medium × medium, and medium × light. The results showed that dark is dominant to medium, and medium is dominant to light, while medium with medium produced three classes resulting in a 1:2:1 ratio, 1 being as dark as the deep medium parent designated as l^{m1} l^{m1}, 2 being medium as F_1, or l^{m1} l^{m2}, and 1 being as light as the light medium parent designated as l^{m2} l^{m2}. As a result of this study, the writer proposed a multiple allelormorphic series as follows: L, l^{m1}, l^{m2}, l. A description of various combinations of genes in this allelic series has been made.

As to the shattering character of pods, there is some difference in the extreme shattering of pods in wild type and semi-shattering of cultivated type. The shattering of the wild type has some dominant effect in the F_2 population, as only one-fourth of F_2 plants held their seeds in pods firmly. Another series of crosses showed that the shattering is recessive, the inhibiting gene or genes being probably involved.

B. Inheritance of Seed Characters

Owing to the complex color pigments involved for seed characters, the study of seed characters is considered quite complicated. A brief review of previous work and some attempts at analysis of some results have been made to clarify this situation. New color types were described. However, in the writer's opinion, some basic problems about the formation and interaction of pigments in a physiological way ought to be worked out to check over genetic details obtained, so that in turn, it will facilitate the work along genetic lines.

Defective seeds were grouped into two types. The seeds of type I are usually with irregular appearance of cracked seed coat, the plant being always with gray hair and the seed with buff or imperfect black hilum; while the seeds of type II are generally with quite regular, net-like cracking on the sides of the seed, no matter what kind of hair color is concerned. In order to test their genetic relationships, the crosses made between type I and normal resulted in three kinds of Phenotypic ratio, namely 3:1, 15:1, and 63:1. From the analysis of F_3 data of a cross showing a 63:1 ratio, the writer agreed with and confirmed the result obtained by Stewart and Wentz (1930), in which an inhibiting gene I for the restriction of color pigments is also responsible for the prevention of the defective seeds causing therefore normal seeds. However, the results also proved that two recessive genes are necessary for

the appearance of defective seeds in type I, along with the presence of recessive gene i.

As to the crosses involving type II, all showed the same results; namely, nearly normal in F_1 and 9 normal to 7 defective in F_2, being just the reverse of the result obtained by Nagai (1926). Either one or two recessive genes, de_3 and de_4, have been suggested as responsible for defectiveness, only the seed with De_3De_4 constitution being normal in the seed coat.

A cross was made between type I and type II. The details showed various degrees of variation of defectiveness. But a definite classification can be made by judging the differences in cracking between types I and II. The interaction of three pairs of defective genes is considered to be as follows: the De_1 gene (for normal in type I) acts partially to prevent the formation of complete net-like cracking on seed coats as shown in the constitution of $De_1De_3de_4$ and $De_1de_3De_4$. Even in the constitution of $De_1de_3de_4$, De_1 still shows some preventing effect, as a lesser amount of network resulted. But those seeds have a marked tendency to form a network, as shown the appearance of a "network"-like structure under the surface of the seed coat. Both De_3 and De_4 genes have a predominant effect to prevent the action of de_1 in formation of irregular cracks on the seed coat as in type I. But de_1 still has an ability to cause some splitting or cracking lines on seed coat.

By this study, genes for defective type I, and genes for defective type II are shown to be quite different, both in their expression on seed coats and in the behavior in inheritance.

As to the pattern on the seed coat, only five kinds of pattern are presented in detail:

1. *Light Brown Ring on Dorsal Sides of Seeds, as in Seneca.*—Three crosses with normal showed the same results. All F_1 seeds were with such light brown ring, while in F_2 the result was 9 seeds with the same character as in Seneca, to 7 seeds without it. Rg_1 and Rg_2 genes are suggested as complementary genes for light brown ring. One thing has been found of importance that all seeds with light brown rings were found on the plants with dark pods. It is supposed that the gene or genes for light brown ring may be completely linked with the gene or genes for dark pods, or the light brown ring may be determined by the gene or genes for pod color.

2. *Light Brown Area Located on the Seed Coat Just above the Radical, as in T140.*—This colored area is usually half fan-shaped, and the terminal point always points to the micropyle near one end of the hilum. Its origin and behavior in inheritance are not clear. Several crosses were made showing this character is dominant in F_1. In one cross made

with the bicolor type, the F_2 showed that the brown area was probably covered by other color pigment. But the brown color still reappeared in certain of the F_2 segregates.

3. *"Spread" Hilum.*—The appearance of "spread" hilum differs from the formation of the saddle on the seed coat in terms of i^k gene. It is mainly due to the extension of the pigments out from the hilum to form a saddle-like pattern over the seed coat. There is no definite margin for this kind of saddle, and it was not so uniform as the normal saddle (i^k). It might be determined by a recessive gene sp for spreading color pigments out from the hilum. But segregation is very complicated, making classification difficult.

4. *Bicolor Types.*—Both black and brown pigments may be present on the seed coat at the same time. One kind of bicolor, as T146, has distinct brown as a basic color, while black rings are formed concentrically around the hilum. In the cross between bicolor and green the F_1 hybrid was quite close to the green parent, while various degrees of coloration have been observed from F_2 progeny. So we may assume that this bicolor type carries genes for both black and brown pigments, as both solid black and solid brown seeds segregated out of the F_2 population.

5. *Flecky or Mosaic Seed Coat.*—The occurrence of both black and brown pigments on the seed coat may result in a flecky or mosaic seed coat, on which black pigments are evenly distributed on the brown base of the seed coat, in the form of small spots. Only a small number of them was found from F_2 and F_3 progeny. No one progeny bred true for this character. Hence no successful conclusion can be drawn without genetic trials. But, by the study of the distribution of color pigments in the F_2 population, it appears that green or yellow is the basic color for the seed coat produced by a certain amount of chloroplasts of yellow pigments, while brown pigment spreads along the surface of the seed coat first, then black pigment later, and this sequence results in various color types.

The inheritance of cotyledon color conforms to the results of Woodworth (1921), as shown in their behavior in segregation in F_2 and F_3. Two recessive genes, d_1 and d_2, are necessary for green cotyledon.

The normal hilum is determined by two dominant genes, N_1 and N_2, while abnormal hilum is considered to have the genic constitution of N_1n_2, n_1N_2, and n_1n_2.

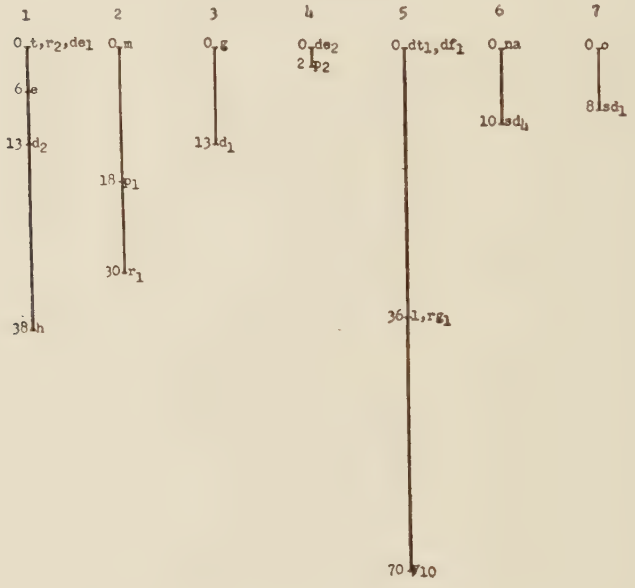
The bloom is a delicate, powdery coating on the seed coat of several soybean types. In the present study, the results of the 3:1 ratio in F_2 indicate that there is only one gene difference between the types involved. The fact that all wild types have bloom is considered important, as this character may impart high ability to resist unfavorable conditions.

C. Analysis of Linkage

A complete and comprehensive review of literature on the linkage studies on soybeans was presented. Theoretically, the linkage groups of soybean should be 20 in number. So far as the present study is concerned, only seven linkage groups have been worked out by several authors. A tentative chromosome map is presented, including all details thus far reported (as shown in Figure 1).

Figure 1

Provisional Soybean Chromosome Map



The first linkage group is the t-e-d_2-h group or chromosome I, e being for late maturity, d_2 for green cotyledon, and h for soft seed coat, r_2 for brown seed coat and de_1 for defective seed coat in type I, being completely linked with t gene for gray pubescence. The position of h has not yet been settled. The second group is m-p_1-r_1 involving m gene for mottling, p_1 for no inhibition to the pubescence, and r_1 for brown seed coat. The third group is g-d_1, g for yellow seed coat, and d_1 for green cotyledons. The fourth group is de_2-p_2, de_2 for defectiveness in type II, and p_2 for glabrousness. The fifth group is dt-l-y_{10} involving dt for determinate growth habit, l for light pod color, and y_{10} for yellow type (as T135). One of the genes for dwarfness (dfl) is completely linked

with the dt gene, while one of the genes for non-stained seed coat (rg_1) is completely linked with l gene. No positional determination has been made on this linkage group. The sixth group is na-sd_4, na being for narrow leaf shape, and sd_4 for 3 seeds per pod with a high percentage of 4. The seventh group is the o-sd_1 group, involving the o gene for oval leaf shape, and sd_1 for 1 seed per pod.

A brief discussion and concise conclusion are presented, dealing with several cases which are quite important to soybean genetics. The main topics are these: interaction of genes, qualitative and quantitative characters, hereditary and environmental factors, and comments on the origin of soybean species. Information gathered by various workers reveals the common occurrence of duplicate genes, as for example d_1 and d_2 for green cotyledon, t_1 and t_2 for gray hair, y_7 and y_8 for yellow plant type, l^{dt} and tf for indeterminate growth habit, wv_1 and wv_2 for wavy leaf type, de_1 and de_2 for defectiveness in type I, and df_1 and df_2 for dwarfness. The writer prefers to draw the conclusion that the ordinary diploid soybean is probably tetraploid in nature, resulting from the duplication of whole sets of chromosomes from an ancestral form with the basic number of 10. As ordinary tetraploids were produced by the treatment of ordinary diploids with colchicine, then if common soybeans were tetraploids in nature, these colchicine-produced tetraploids are octoploid. Hence, no successful cross can be made by crossing between octoploid and tetraploid soybeans.

A complete list of genes in soybeans, so far as the present study is concerned, is presented below.

LIST OF GENES IN SOYBEANS

Symbol	*Characters*
A	Appressed or twisted pubescence; a, erect pubescence
B_1, B_2, B_3	Complementary genes for bloom on seed coat; either b_1, b_2, or b_3 for non-bloom on seed coat
D_1, D_2	Duplicate genes for yellow cotyledons; d_1d_2, green cotyledons
De_1, De_2	Duplicate genes for complete seed coat; de_1de_2, defective seed coat accompanied with I *vs.* i acting as triplicate genes in type I
De_3, De_4	Complementary genes for complete seed coat; either de_3, or de_4, or both, for defective seed coat in type II
Df_1, Df_2	Duplicate genes for normal plant height; df_1df_2, dwarf plant (Df_3~*vs.* df_3 might act with Df_1 and Df_2 as triplicate genes resulting in a ratio of 63:1; or I^{dt} *vs.* i^{dt} exist for inhibition on growth habit; or one of genes for determinate growth habit reacts with dwarf genes)
Dt	Indeterminate growth habit; dt, determinate growth habit
F	Normal stem development; f, fasciated or flattened stem
Fc_1, Fc_2	Complementary genes for normal length of flower cluster; either fc_1, or fc_2, or both, for long flower cluster

Symbol	*Characters*
G	Green seed coat; g, yellow seed coat
H	Hard seed coat; h, soft seed coat
I, i^h, i^k, i	Multiple allelomorphic series for inhibition of black and brown pigments in seed coat I, total inhibition; seeds show no black or brown pigment even in hilum i^h, partial inhibition; permits pigment only in hilum i^k, partial inhibition; permits pigment extended out from the hilum to form saddle pattern on seed coat as Black Eyebrow i, no inhibition; seeds are solid black or brown
I^{de}	Inhibiting gene to prevent the formation of cracking on seed coat in type I, identical with I as suggested by Stewart and Wentz (1930); i^{de}, no inhibition, identical with i
I^{dt}	Inhibiting gene to prevent the plant making indeterminate growth; i^{dt}, no inhibition. It reacts with Tf *vs.* tf for terminal flower cluster as duplicate genes.
I^p	Inhibiting gene to prevent the appearance of hairs on plant, identical with P_1; i^p, no inhibition, identical with p_1
I^t	Inhibiting gene to prevent the presence of tawny hair color; i^t, no inhibition
L, l^{m1}, l^{m2}, l	Multiple allelomorphic series for pod color L, dark color, as black, dark brown, etc. l^{m1}, deeper medium color, as deep brown, goldenish brown, etc. l^{m2}, lighter medium color, as light brown l, light color, as tan, straw yellow, very light brown, etc.
M	Mottling, or bicolor seed coat; m, no mottling
N_1, N_2	Complementary genes for normal hilum; either n_1, or n_2, or both, for abnormal hilum
Na	Normal leaf shape; na, narrow leaf shape
O	Normal leaf shape; o, oval leaf shape
P	Pubescence, identical with P_2; p_1, no pubescence, identical with p_2
R	One of two complementary genes, R and T, for the presence of black pigment on hilum and seed coat, identical with R_1; r, brown hilum, or brown seed coat
Rg_1, Rg_2	Complementary genes for stained seed coat or light brown ring on seed coat as Seneca; either rg_1, or rg_2, or both, for non-stained seed coat
S	Tall, late-maturing type; s, stocky, early-maturing type
Sd_1	Normal 3-seeds-per-pod; sd_1, 1-seed-per-pod
Sd_4	Normal 2-seeds-per-pod; sd_4, 3-seeds-per-pod with higher number of fours
Sh_3	Non-shattering of T135 dominant to the shattering of Gracilis; sh_3, shattering of Gracilis
T	Tawny pubescence color; t, gray pubescence color
T_1, T_2	Complementary genes for tawny pubescence color; either t_1, or t_2, or both for gray pubescence color
Tf	Formation of terminal flower cluster at the tip of plant; tf, no terminal flower cluster formed
V_1	Normal chlorophyll distribution; v_1, variegation
W_1, W_2	Complementary genes for purple flower; either w_1, or w_2, or both for white flower
Y_8	Normal green plant; y_8, yellow-green leaves in seedling stage, becoming goldenish yellow-green at maturity
Y_{10}	Normal green plant; y_{10}, yellow-green leaves existing through all stages of plant growth

VITA

The author was born on December 4, 1915, on a farm near Kuantang-chueh, Tesitian, Hanyang, Hupeh, China. In 1932, he attended Hupeh Provincial Senior Middle School in Wuchang, China. He graduated from there in 1935 with an honorary grant offered by his Provincial Government. In the same year, he was permitted to enter the Department of Agronomy in the National Central University, Nanking, China. He held a University Scholarship from 1937 to 1938. In October, 1937, he was forced by the Japanese invasion to move westward with his school from Nanking to Chungking, China. He was graduated from that University with the degree of Bachelor of Science in 1939.

Since then, the writer was appointed in that University as Assistant in the Department of Agronomy from July, 1939, to June, 1943. During this period, he also taught biology in Chungking Municipal Middle School for one year, took charge of College Farm for two years, and served as an instructor to teach Farm Project for college students. In July, 1943, he was asked to be a technician in Agronomy in the Ministry of Agriculture and Forestry. He held this position until he got the chance to go abroad.

By passing the qualifying examination in November, 1943, he was awarded a fellowship by his Provincial Government. He arrived in the United States January, 1945. In February, 1945, he matriculated at the Graduate College of the University of Illinois, and completed work for the degree of Master of Science in February, 1946. He held a University tuition scholarship and a grant from the China Institute in America in 1947.

The writer is affiliated with the Chinese Society of Agricultural Science, Chinese Society of Agronomy, American Society of Agronomy, American Soybean Association, American Association for the Advancement of Science, and Sigma Xi honorary society.